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XXIX.—*The Coloration of Marine Animals.* By W. C. M'Intosh, Professor of Natural History in the University of St. Andrews *.

The coloration of marine animals has long formed the theme of many a descriptive text and ancient figure—in which sea-flowers, sun-stars, purple urchins, gorgeously iridescent annelids, blue and red crabs, the very varied and beautiful tints of shellfishes and cuttlefishes, and the endless hues and resplendent lustre of fishes were each in turn portrayed. Some of the old authors even went into the origin and meaning of such tints. On the present occasion, however, it is not so much the abstract beauty everywhere so prevalent in the coloration of marine animals (and these chiefly British) which will form the subject of our attention, but rather the application of certain recent theories to the explanation of the tints so characteristic of many marine animals.

As indicated, the older naturalists in many cases clearly recognized the connexion between the tints of an animal and its surroundings. It was reserved for the illustrious Charles Darwin and other distinguished naturalists, such as Mr. Wallace, and many of the younger zoologists who follow in their footsteps, to endeavour to explain the production and modification of the tints of land-animals (the term being used in its

* The Introductory Lecture for Session 1900-1901.

widest sense, so as to include birds) by Natural Selection and Sexual Selection. Moreover, the subject has been treated under such heads as *Protective Resemblance*—that is, the tints enable an animal to escape its enemies; *Aggressive Resemblance*—that is, the tints aid in capturing prey; *Protective Mimicry*—a condition in which an animal is mistaken for another, and thus, as it were, lives on the reputation of another; and, lastly, *Warning Coloration*, as exemplified by conspicuous coloration in an animal having an unpleasant attribute. Besides these subdivisions there are other cases in which special markings occur on an animal, apparently for recognition (for instance, the white tail of the rabbit) or for the purpose of diverting attack from a vital part (for example, wings of butterflies). In certain cases none of the foregoing causes exist, and these have therefore been termed cases of typical coloration. The facts and arguments brought forward in support of the foregoing views will have the more weight if it be found that similar features are met with in the mammals, fishes, and invertebrates inhabiting the ocean. The sea offers a very different environment, however, from the land, since it is continuous throughout its vast extent, so that it is possible for animals to pass from one region to another without the presence of those formidable barriers which, for example, restrict the land-mammals to certain isolated regions of the earth's surface. Yet if Natural Selection or Sexual Selection be held responsible for the coloration in the one case—that is, on land—it is difficult for either to escape similar responsibility in the marine forms.

Again, it has to be remembered that light, aeration, and an abundant supply of food have a connexion with animal coloration, as may be observed in the subdued tones in the Nudibranchs and in anemones, either from deep or shallow water, after confinement.

In dealing with the coloration of marine animals under the several classes it will suffice to divide them severally into two great groups, a classification which has been of service on former occasions, viz.: (1) pelagic, that is, swimming or floating animals, and (2) demersal, or forms which frequent the bottom of the sea. This division is truly one of convenience, since the two groups are closely connected, some in their young state being pelagic whilst they are demersal in their adult; others, again, though perhaps springing from pelagic young, generally live on the bottom till they put on their nuptial dress, when they swim freely in the water, scattering their eggs all around and then perishing.

Amongst the simplest marine animals colour is often

present. Thus A. Agassiz notes that the pelagic Globigerinæ floating in masses are occasionally tinted reddish or scarlet, and pelagic Infusoria, like *Ceratium* and *Peridinium*, are of a greenish or reddish hue. In such forms the influence of Natural Selection or other cause just indicated would appear to be slight.

It cannot be said that the bright yellow, white, purple, red, and brown hues of littoral sponges, or the blue or pinkish-purple of deep-sea sponges, are due to Natural Selection—not more, indeed, than the tints of the calcareous corallines. Mr. Garstang's view that they are thus conspicuously coloured because they have a nauseous taste is balanced by the fact that many are of an extremely sober tint, and that numerous palatable animals are equally conspicuous in their hues. Moreover, the common crumb-of-bread sponge assumes, under the same circumstances, various hues in the tidal region, such as brownish, purplish, yellowish, and greenish. The white colour of *Grantia compressa*, *Leuconia nivea*, and the occasional purple of *Leucosolenia botryoides* are also devoid of relation to their surroundings. Further, tufts of *Chalina* and *Suberites* are occasionally found in the stomach of the cod, and sea-lemons browse upon sponges of various hues. The opinion of the author just mentioned that the association of the red *Suberites* (which, like other sponges, is, he says, intensely disliked by fishes) with *Pagurus cuanensis* is for the benefit of the crab may be true, but *Suberites* is brownish or stone-coloured in some cases, and does not always protect the crab from fishes. The view that some crustaceans, a group so much sought after by fishes, escape capture by dwelling in sponges (Garstang and Poulton) needs confirmation. Many annelids and some z ophytes are found in sponges, but it has generally been thought that they occur there just as they occur under compound ascidians, tangle-roots, and *Melobesia*—viz. for protection. In like manner the crustaceans and annelids found in the interior of Venus's flower-basket are there for shelter, not because the sponge is inedible.

In considering these views of the coloration of sponges it would seem to be as legitimate to state that the forms of *Chondrocladia virgata* and *Cladorhiza pennatula* (which, for the moment, may be supposed to be palatable) were specially given them for protection, since they escape search in the one case by resembling the backbone of a fish and in the other a tiny pinnate zoophyte.

It is generally stated that the surface-fauna of the ocean is transparent or faintly coloured, apparently for the sake of

protection, but it seems to have been overlooked that many of the surface-animals are there only for a limited period during fine weather, and disappear into the depths on the advent of storms and cold. Moreover, not a few of the forms disporting themselves at the surface are conspicuously coloured—for example, the jellyfishes *.

Protective coloration, by which is meant that hue in harmony with the surroundings, and which, for instance, causes a very young leveret on the approach of danger instinctively to leave the green sward and crouch on the brown earth to escape observation, reaches its acme in the transparent tissues of the jellyfishes. There are, however, many exceptions, and even the most transparent forms by-and-by develop opaque bands (the ovaries and spermaries) just when the existence of the organism is most valuable. The brightly coloured forms again, such as *Oceania*, *Pelagia*, *Velella*, *Porpita*, and many others, which follow precisely the same habits as the uncoloured and transparent, raise doubts as to the validity of the interpretation so generally accepted. These doubts, indeed, find expression in Prof. Moseley's remark that deep blue forms are so coloured for protection. Deep blue jellyfishes, however, form but a small proportion of the vast numbers found in the ocean. Neither are the varied hues of any advantage as warning colours, for the brightly coloured and the translucent (as Beddard remarks) are equally palatable to whales and other forms (not excepting man) utilizing them for food. The pelagic sea-anemones are also coloured, and the floating stages of others (*Arachnactis*) are often tinted with white and yellow.

The brilliant colours of anemones in general cannot be said to be either protective or warning, since on the one hand there is no more deadly bait for cod, and on the other many small fishes swim in comfort in tanks amongst anemones, and in the China Sea a red fish takes shelter in the stomach of an anemone two feet across. Anemones for the most part seem to defy protective coloration, as is sufficiently proved by a glance in the rocky caverns on the eastern shores or along the creeks of the west, where the olive-green tangle-blades and other seaweeds are studded with the opelet (*Anthea cereus*), whose long trailing tentacles, with their hues of green and red, wave with every surge of the tide. The view that the gaudy

* Beddard observes:—"If transparency of pelagic organisms, according to Darwin, be due entirely to Natural Selection, it is remarkable that there is so little modification in this direction amongst the species inhabiting the bottom" (*op. cit.* p. 126). He is inclined to think that protective resemblance may be due to other causes than Natural Selection.

colours of anemones act as a warning is not borne out by the eagerness with which the cod swallows the brightest, such as *Stomphia*, while the smaller flatfishes fill their stomachs with *Edwardsiæ*.

Thus it would appear that mechanical protection is mostly subserved by the bag of small anemones around the caudal extremity of the Indian hermit-crab, *Chlænopagurus Andersoni*.

The red of *Tubipora* and the coral of commerce, the varied tints of coral polyps, in which green of many shades predominates, the blue of *Heliopora*, the purple of *Pennatula*, the reddish or pink colour of *Tubularia*, *Coryne*, and *Syncoryne*, and the long chain of reddish-orange polypites of *Diphyes* as it darts hither and thither amongst the bluish masses of floating oceanic animals with much greater speed and certainty of direction than usually shown by them, and even seems to elude the hand-net or the dipping-bottle, appears to have as little to do with protection or warning as the green of *Rhizosolenia* or the red of the wild poppy. Nor does sexual selection appear to be exercised in the group, though in some, as in the American *Aurelia flavidula*, the female has yellow ovaries, while the male shows roseate spermaria. Nor is the habit followed by *Tealia crassicornis* in coating its column with gravel (as some sea-urchins do with their bodies), or still more conspicuously with white shell-fragments, in harmony with the views concerning warning coloration.

The colours of Echinoderms are often most conspicuously bright, as, for instance, the blues, reds, and purples of Asteroids, the blues, reds, and variegated red and white of Echinoids, the reds and purples of Crinoids and Ophiuroids. It may be that it is in consequence of these bright colours that some authors have fancied that sea-urchins exhibit protective measures when they cover themselves with bits of pebble and shells; but the same, as already explained, occurs in anemones.

The brilliant orange-red of *Hippasterias* in deep water may subserve a purpose unknown to us, yet from analogy this is unlikely. Few forms are more conspicuous on the bottom of the sea or on the blades of tangles at low water than the common cross-fish, yet gulls, fishes (cod and catfishes), and an ally of its own (the sun-star) devour it. Thus, while its coloration is certainly not protective, it does not seem to serve as a warning or to be the result of Sexual Selection. The brilliant scarlet of *Solaster papposa* as it hangs on the tangle-blades makes it very conspicuous, but there is no evidence either as to protective or warning properties. The same may

be said of the purple or orange hue of *S. endeca* from deep water and of *Cribrella sanguinolenta* between tide-marks. The sand-stars (e. g. *Ophiura lacertosa*) are often tinted of a hue resembling their surroundings, yet they and the more brightly tinted forms are common in the stomachs of fishes and are eagerly devoured by gulls when stranded on the beach.

The common sea-urchins of our own shores are often conspicuous on the tangles at extreme low water, and their tints are neither protective nor warning as regards man and certain fishes. Though some species (e. g. *Strongylocentrotus lividus*) show sexual differences, the male being darker and the female of a violet tint more inclined to red, Sexual Selection need scarcely be considered. The burrowing habit of the species just mentioned would seem to indicate that its colour was neither protective nor warning. The colours and habits of the heart-urchins give the same lessons. Amongst others the green-pea urchin is a favourite food of the haddock.

The brown and purple hues of the sea-cucumbers may in some way subserve protection amongst the dark masses of the tangles, yet both they and the transparent forms are found in the stomachs of fishes. In the purple forms in the deep sea Prof. Moseley is of opinion that the colouring is useless, "and is merely due to the persistence of colouring developed originally in shallow-water ancestors." But there may be other explanations which are less theoretical, especially as the same purple colour is found in a feather-star in shallow water in the tropics and in a sea-cucumber in 1955 fathoms in the antarctic sea.

The transparent Holothurians and the Synaptidæ are often almost colourless, so that the arguments in connexion with coloration do not fit.

No group is more beautiful or more varied in coloration than the marine Annelids, and no group of Invertebrates offers a better field for the manifestations of protective resemblance, for the display of warning coloration, and, since the sexes in the majority are separate, for the operations of Sexual Selection. Yet some of the most brilliantly tinted, like the sea-mouse, frequent muddy sand or mud, where the metallic lustre of their resplendent bristles would only betray them; and the same may be said of some of the most conspicuously coloured Hesionidæ, e. g. *Ophiodromus*. It is true the bright colours and iridescence of many are hidden within tubes, but this would rather point to coloration in these cases being independent of protection. Even in forms that dwell in sand, like *Nephthys*, *Ophelia*, and *Magelona*, the iridescent pearly

lustre or the flesh-tint by no means resembles their surroundings, whilst other dwellers in sand, viz. *Phyllodoce maculata* and *Autolytus rosea*, are finely coloured. Forms frequenting the fissures of rocks or tunnels in calcareous algæ are equally varied in tint, from the sombre grey of *Trophonia plumosa*, the deep green of *Eulalia viridis*, the straw-coloured body and red branchiæ of *Morphysa*, to *Lysidice* with its madder-brown anterior end and white collar. Those having finely coloured plumes anteriorly, like the Sabellidæ, occupy tubes, and in few instances are their plumes in harmony with their surroundings. One instance, however, is given by Prof. Semper * of agreement between an allied form (*Myxicola*, one of the Eriographididæ) at Port Mahon and a coral (*Cladocera*). Both the polyps and the funnel of the annelid were of the same chocolate-brown colour, and thus at first sight protective resemblance might have been diagnosed; but the annelid also occurred in a sponge of a totally different colour and in clefts of rocks where no tint resembled it. When Semper tapped the coral the annelids retracted their plumes at once, but the corals remained expanded. There was really no protective resemblance. Dr. Eisig mentions an *Eunice* parasitic in a sponge of a yellow colour, the annelid being yellow with orange spots, and he considers this an instance of protective coloration, though Beddard thinks the tint arises from feeding on the sponge. As, however, these annelids generally construct a tough parchment-like tube in sponges, the example is dubious. Two annelids, *Euphrosyne* and *Spinthes*, are also partial to yellow sponges, on which they feed and they may be held to be protectively tinted. Some Polynoidæ with mud-covered scales approach the hue of the muddy inner surface of shells dredged from deep water, or the muddy inferior surface of stones between tide-marks. The dorsum under the scales and the free parts of the body posteriorly in others are coloured conspicuously with brown bars, so that the case may fairly be claimed as one of protective adaptation. *Malmgrenia*, commensalistic on purple urchins, also agrees with its surroundings, being tinted of a deep purple, and the polynoid in the interior of *Euplectella* is more or less translucent. On the other hand, *Nereilepas*, commensalistic with the hermit-crab in the great whelk, is conspicuously tinted.

Pelagic annelids, again, are not always colourless, even the Alciopidæ having finely coloured eyes. The pelagic stages of *Autolytus* so common in various seas are often coloured both green and pink. Little change in the tint of the green

* *Vide* Beddard.

Palolo takes place for its pelagic stage, and the hues of the pelagic phases of the Nereides are likewise vivid. The colours of the pelagic young of the sedentary forms, such as *Sthenelais*, are often brightly coloured.

Annelids which perforate hard substances, as *Polydora* and *Dodecaceria*, are coloured equally with the free, and the pelagic phases of the latter retain vivid tints.

The Nemerteans and other Turbellaria, with a few exceptions, such as *Nemertes carcinophila*, are often of a colour at variance with their surroundings—and the same may be said of the Leeches; but the Gephyreans, especially those frequenting mud, are generally inconspicuous, though *Bonellia* is green. The marine Planarian *Eurylepta vittata* between tide-marks is conspicuously banded with brown and yellow, and others are similarly variegated with red, purple, and yellow. Many, however, are of a uniform colour and often resemble their surroundings. As anemones and fishes prey on them, their colour would not seem to be protective, either in the sense of corresponding with their environment or acting as a warning to predatory forms. Mr. Punnett tells of a small Nemertean parasitic in an Ascidian which is brightly striped, and larger free species are similarly banded. *Borlasia Elisabethæ*, which is boldly blotched with purplish brown and white, lives in a tube of mud under stones in Herm.

The coloration of the sexes in the Crustaceans is often similar, as in the common and the Norway lobsters, though in some (*e. g.* the shore-crab) there are marked differences. Yet after all what selection can a female shore-crab exercise when the courting is carried on when she is in a soft and helpless condition immediately after casting her shell? The minute complemental males of certain Cirripedes afford similar data.

The evidence in regard to protective coloration is somewhat ambiguous. On the one hand, Prof. Moseley states that the Crustaceans (*Nautilograpsus*) found on the gulf-weed resemble it in tints, even to the white patches which imitate those of *Membranipora* and the sea-acorns (*Balani*). He also records a similar crab of a blue hue on the float of *Janthina*. *Portumnus variegatus* somewhat resembles the greyish hue of the sand amongst which it lives. The coloration of the stalk-eyed crustaceans is often curiously complicated by parasitic growths, such as algæ and zoophytes. Even the slender *Stenorhynchus rostratus* has its dorsum and limbs enlivened by tufts of *Ulva* or by *Plumularia*, *Campanularia*, patches of *Halichondria*, and the tubes of *Terebellæ*.

The modification of the natural hue is thus considerable. Yet *Hyas araneus* far surpasses it in the number and variety of its parasitic growths, that of young specimens from cavern-roofs resembling the dorsum of *Aphrodita*. As the hue of this species is brownish purple or reddish purple, it might be supposed that the extraneous growths would be protective. *Hyas coarctatus* is even more subject to such growths, yet both, covered with parasites as they are, abound in the stomach of the cod, which pays scant attention to coloration. *Hippolyte* in the rock-pools of St. Andrews often differs from the tints of the seaweeds it frequents. Again, why should the female *Pinnotheres* in the horse-mussel be so brightly coloured, the male being less conspicuously so? Both are equally protected. Many pelagic crustaceans are also more or less translucent. *Mysis flexuosa* is grey when on sand, brown or green when amongst seaweed of these two colours. The gribble, whose sole function is to perforate wood, and thus is constantly sheltered, is more soberly tinted than, for instance, other Isopods, such as *Sphæroma* in fissures of rocks, which has its under surface speckled with white, legs with brown, and head with brown, white, and red. *Hyperia galba* in the gastric cavities of *Aurelia aurita* is often reddish brown. Brightly coloured crustaceans like *Dexamine spinosa* are eaten by fishes. The pelagic *Zoeæ* have conspicuous greenish-blue eyes, and the pelagic young of *Crangon* are brightly tinted. *Caprella tuberculata*, again, occurs in swarms on *Ceramium rubrum*, and is of the same tint. *Idotea pelagica* on *Ceramium rubrum* is sometimes beautifully speckled with white in marginal scallops or central streaks, and is thus more conspicuous than usual. *Podocerus pulchellus* frequents the same seaweed, with which it harmonizes in colour; but here, again, it is sometimes gaudily tinted with reddish brown and white, so as to be conspicuous. Many sessile-eyed crustaceans are beautifully tinted, like *Montagua monoculoides*, with reddish-orange or orange specks in rows on the dorsum, and others are marbled with brown and white. The pelagic *Eurydice pulchra* and *Janira maculosa* of our seas are not inconspicuous in coloration.

On the other hand, many land-crabs, such as *Ocypoda*, as Prof. Moseley tells us, are tinted of a bright red or other conspicuous hue. The reddish Norway lobster frequents greyish mud, from which the cod picks it up so readily. The common shore-crab is often variegated with white in the brackish inlets of the Outer Hebrides. The reddish-orange *Alpheus ruber* is as conspicuous as it can be in the tidal pools of Herm. The multitudes of the sand-hoppers are white and

easily seen amongst dried sand and seaweeds. The parasitic cirripede on whales (*Coronula*) retains its white colour, and *Lepeophtheirus* on the salmon and *Caligus* on the cod each have their brownish-olive hue and are readily seen on the skin.

Some pelagic crustaceans (Copepoda) are of a deep blue or brilliant scarlet, and the young pelagic stages of many of the higher Crustacea are marked with vivid tints. The pelagic barnacles are not inconspicuous. Even the translucent *Phronima* (Amphipod) has three sets of conspicuous eyes. Prof. Moseley describes the deep-sea shrimps and schizopods as of an intense bright scarlet colour. A deep-water *Serolis*, again, described by Mr. Beddard is blue.

There is no evidence that the tints in any of those conspicuously coloured act as a warning, since they are found in the stomachs of fishes equally with those of sober tint. The diurnal changes of hue in such as *Hippolyte* are, moreover, not always explained by their environment *.

The Brachiopods are generally pale, yet *Lingula*, an ancient type which frequents sand, has its valves tinted of a fine greenish hue.

Some of the Polyzoa are brightly coloured, e. g. *Bugula*, which is purple, whereas others, such as *Gemellaria*, have a uniform pale straw-colour. *Membranipora* is conspicuous by its pale lacework on the blades of the tangles. The majority of the Polyzoa, *e. g.* the *Lepraliæ*, have no vivid coloration, though some are pinkish, and so with *Flustra*. Their colour does not appear to have any relation to Natural Selection and is neither protective nor warning—not more so than the purple of the alga *Corallina officinalis*.

While the adult *Phoronis*, which is tubicolar, is either pale or with dark brownish tentacles and pale body, the pelagic young (*Actinotrocha*) is brightly tinted. This might be explained by supposing that these tints are ancestral and that former conditions may have necessitated them. Such, however, is conjecture, as also is the view that disadvantageous colours in the young have little time to do harm.

The colours of the next group—that of the shellfishes—have long been a source of interest; and as they affect both the hard and the soft parts, their study might be supposed to throw some light on the questions before us.

Comparatively few examples of protective coloration occur amongst the bivalves, the calcareous valves of which, perhaps,

* *Vide* on this subject the valuable paper by Messrs. Gamble and Keeble, Quart. Journ. Micr. Sc. vol. xliii. pp. 589–698, pls. xxxii.–xxxvi. (1900).

and the enormous powers of reproduction, suffice in some cases for safety. Those which perforate rocks, wood, and other media are, as a rule, white, yet the date-shell (*Lithodomus*) has dark brown valves, whilst *Modiolaria* in the tests of Ascidians and in sponges is feebly tinted. The species which burrow in sand have diverse and often bright tints, such as *Psammobia* and *Tellina*, dull brown, as in *Cyprina*, or pale, like the cockle and *Thracia*. Littoral forms are likewise varied. The mussel is dark blue or purplish blue on mud or rock; *Galeomma* with its outspread valves on the under surfaces of stones is pure white, *Arca* in the chinks of rocks is dull grey, and *Lima hians* has brilliant orange fringes, but the animal makes a nest. The beds of sedentary dull greyish oysters and the brownish-black horse-mussels in the adjoining area under water are in contrast with the more brightly tinted and free scallops in similar regions.

There is endless variety under the same circumstances, but no certainty as to protective or warning coloration or sexual changes in the valves of marine forms.

It is interesting that pelagic young mussels and the slightly older forms which settle on zoophytes in myriads are differently tinted from the adults. The latter (young mussels) especially harmonize with their surroundings. The pelagic young of marine lamellibranchs (after the formation of the shell-), indeed, seem to approach each other more or less closely.

The parasitic bivalves, like *Montacuta substriata* on *Spatangus purpureus*, are in harmony with their surroundings, though as regards coloration they are pale and more or less transparent.

Coloration in the univalves (Gastropoda) has no apparent relation to their acceptability to forms which prey on them, and therefore has no protective or warning functions. All the available smaller forms—whatever their colour may be—are equally palatable to the haddock, which, as Edward Forbes said, is a great conchologist. In their pelagic stages, it is true, they are less brightly tinted, and thus may be held to be protectively coloured; but other young forms, which are not pelagic, are of similar pale or neutral hues, so that there is room for doubt. The question may well be asked, Are the bold bluish iridescent streaks of *Helcion pellucidum* equally protective or warning in the young on the dark blades of the tangles in the rock-pools, and on the adults hidden under the hard roots of the same seaweed?

Protective coloration in the Gastropods is exhibited by *Ovula patula* on *Gorgonia verrucosa* (Poulton) and *Ovulum*

uniplicatum on *Leptogorgia*. *Hermæa*, a transparent Nudibranch on a reddish weed (*Griffithsia*), has a reddish outline and a greenish aspect on green seaweed. This coloration is probably due to the contents of the intestine. Some mollusks, like the limpet, chiton, periwinkles, and certain Nudibranchs, are more or less in harmony with their surroundings; and the same may be said of *Trochus lineatus* on the granite rocks of Cobo Bay, Guernsey. A red *Doris*, probably *D. concinna*, frequents *Hymeniacidon sanguinea*, and *Xenophora* attaches fragments of shell, rock, and coral to the edges of the growing shell, and thus resembles its surroundings. The common and Johnston's sea-lemons (*Archidoris tuberculata* and *A. Johnstoni*) may, as insisted on by Prof. Herdman and Mr. Garstang, be protectively coloured so long as they remain contracted and quiescent. Yet it must be noted that the colours of *A. tuberculata* vary, some being gaily tinted with yellow and purple, others, especially under large stones in tidal pools, having more sober hues. Moreover, the species is found not only on the surfaces of *Halichondria*, on which it feeds, but under ledges amongst the red *Styela grossularia* and zoophytes, under large stones, and occasionally on the surface of rocks and *Fuci* at low water. It must also be borne in mind that *A. Johnstoni* accompanies it in its haunts, especially on *Halichondriæ*, the hues of which it much more closely resembles than *A. tuberculata*. It may well be asked why the latter has not more closely adapted itself to the colour of the sponges on which it feeds.

Again, the smaller examples of *Doris repanda* are "of a pure waxy semitransparent white" (Alder and Hancock), and the largest are dusky yellowish, colours which are conspicuous in a rock-pool, especially as they sometimes crawl on the blades of *Fuci* fringing the margin. The border of the mantle in many is injured, as if a portion had been removed. *Doris aspera*, which occurs under stones near low-water mark, is equally prominent, most being white, though a few are yellow. The tints of the abundant *Doris bilamellata* likewise do not seem to be protective between tide-marks, where they are met with all the year round, as is the case also with the conspicuously whitish *Goniodoris nodosa*, usually found under stones in tidal pools. These and the brilliantly coloured *Triopa claviger* are at once detected when the stone is upturned; but they are not wholly confined to such localities, and all are occasionally tossed on shore by storms on the blades or roots of tangles. If some would hold that the conspicuous whitish coloration is thus shielded by their habit of living under stones, what is to be said of their associate *Ægirus punctilucens*, which

specially delights in the dark surfaces of stones in rock-pools from low-water mark to some distance above half-tide? The unpractised eye would certainly mistake these rough little lumps for muddy and stunted masses of zoophytes and debris. How are their gem-like dots of pigment to be explained? Rarely *Ægirus* has been found crawling just under the water-line in a sequestered pool. *Polycera quadrilineata*, *P. ocellata*, and *Ancula cristata* all occur under stones in quiet rock-pools, and are not difficult to detect in their habitats. It is doubtful if they are in want of protective or warning coloration in such places, especially when it is found that in these localities *Doto coronata*, which swarms on the branches of *Sertularia pumila*, requires careful and minute inspection to detect it. It is pale and devoid of much of the beauty of the deep-water specimens so often tossed on shore on the blades of the tangles covered by forests of *Obelia geniculata* or on *Hydrallmania falcata* brought in by the fishing-boats. A clearer case of harmony with environment, however, is that of *Tritonia plebeia* on *Alcyonium*, yet it is readily seen when frequenting *Obelia geniculata* on the blades of tangles.

On the other hand, the dog-whelk between tide-marks is fairly conspicuous, and so is the cowry, especially when the soft parts are protruded. The colours of the Eolids are remarkably bright, and cannot therefore be protective in so far as being in harmony with their surroundings. It has yet to be proved that they are warning colours, for it needs a considerable amount of inedibility to scare a hungry fish, and the cod does not respect this property (if it exists) in *Eolis papillosa*. Fishes which are partial to anemones might be supposed to be careless of the nematocysts of Nudibranchs. Further, the haunts of the Eolides and an attentive survey of their coloration leads to no conclusive results. The amethystine and ultramarine hues of *E. coronata* and the scarlet or bright brick-red of *E. rufibranchialis* seem to have no relation to their surroundings, and does not prevent their being devoured by their hungry fellows when disabled or dead. The same may be said of the fine purplish and the orange varieties of *Eolis Farrani* and of *E. Adelaidæ*. The smaller *Eolis olivacea* and *E. viridis* are not so easily seen on the under surfaces of the stones they frequent; but immersion of these in sea-water readily shows them.

Prof. Herdman, who has given much attention to the colours of Nudibranchs, truly considers that "the red-brown" hues of *Dendronotus* effectively conceal it. Some, however, are brightly tinted with scarlet and rose-pink, and a splendid white variety is common in the same haunts in deep water

and occasionally between tide-marks, while a third is pale and more or less translucent. Moreover, the eggs of Nudibranchs are generally conspicuous.

The pelagic Gastropods also offer very varied coloration. Some are pale like *Spirialis*, others, darker like *Limacina*, show orange-pink like *Clione*, deep blue like *Glaucus*, purple like *Janthina*, or a glassy translucency like *Carinaria* and *Pterotrachea*. If, in the open ocean, translucency be a protective attribute of such forms, it cannot be held that the tinted species conform to this view. Prof. Moseley, again, considered that *Janthina* and *Glaucus* (like *Velella*) are coloured blue for protection, since they thus resemble oceanic water. There appears, however, to be no general feature in the pelagic stages of the group that would point out translucency or a particular colour as the result of natural selection and of importance to the species.

If translucency or a bluish tint are to be held as protective to oceanic forms, the pelagic cuttlefishes do not fulfil these conditions, for the play of colours, like those on "shot silk," occurs throughout the whole series. Moreover, though courtship is known to take place, and though the sexes offer certain external differences in structure, yet the colours are, as a rule, the same in both sexes; so that, in these comparatively intelligent and active Invertebrates, the long ages of Sexual Selection have effected no evident change in coloration, whatever may have been accomplished in other respects. The young forms on escaping from the egg are pelagic and have the same pigment-corpuscles as their parents, though, perhaps, they may be fewer in number.

In the group of the Urochordates the translucent chains of *Salpæ* have been cited as instances of protective coloration; but the chains are readily seen in clear sea-water from the surface to the bottom, in several fathoms, probably 5 or 6. Moreover, the gulls readily strike the surface-forms and remove the nuclei containing the vital parts of the animal. Prof. Moseley thought that some *Salpæ* had a blue and others a brown nucleus for protection, but experience proves that both are equally liable to the attacks of gulls. The translucent *Pyrosoma*, again, is phosphorescent, and it cannot be supposed that it has this property to lure other forms to destruction, since it derives nourishment from minute plants and animals carried in currents of water.

The Ascidians (*Ascidia scabra*) attached to the blades of the seaweeds in the Outer Hebrides, and to various structures in deeper water elsewhere, are brightly coloured; yet this is not protective, as they are most conspicuous, nor can it always

be a warning colour, as Mr. Garstang supposes, for some fishes eat them. The tadpoles of such forms as *Styela* are pink. *Clavelina* shows bright orange and yellow, and bright green characterizes *A. intestinalis* in tangle-roots and similar places between tide-marks, and *A. depressa* under stones in rock-pools. If the red hue of some Ascidians, e. g. *A. scabra*, is assumed to be a warning colour, what is to be said about such as *Molgula*, a colourless form, invested by a thick layer of gravelly mud or sand?

Is the dull red of *Styela grossularia*, projecting here and there through a layer of *Halichondria panicea* on the roofs of sheltered caverns, in the same category in regard to warning coloration as *Ascidia scabra* on the floating blades of the tangles?

The pelagic Appendicularians and their houses are generally translucent, but some are pinkish. Their vast numbers, however, are little in need of protection.

The Compound Ascidians, such as *Botryllus*, *Botrylloides*, *Leptoclinum*, and *Aplidium*, are often strikingly coloured, such as the yellow stars of *Botryllus Schlosseri*, the white surface of *Leptoclinum durum*, or the cinnabar colour of others; yet this does not appear, so far as observations go, to be either for protection or warning. Fishes bite off the sea-weeds on which some grow and swallow them.

Certain Cyclostomes, like *Myxine*, living in mud are of a flesh tint or purplish, as in *Bdellostoma*, while the river-lamprey is olive and the marine boldly mottled with bluish grey and black. *Myxine* has no warning tint, yet its abundant mucus is most offensive.

Amongst Fishes the bony forms (Teleostei) are, on the whole, the most brightly coloured, the Elasmobranchs being more soberly tinted. In some bony fishes both sexes are brilliantly coloured, in others only the male. One general rule, with a few exceptions, prevails throughout the series, viz. that the dorsum is dark and the under surface pale, apparently for protection, the explanation usually given being that, looked at from above, the dark dorsum renders the fish more or less obscure, whereas looked at from below the white or pale under surface is invisible against the sky. Yet *Cottus scorpius* in rock-pools occasionally has the head pale orange and the dorsum speckled with the same colour, and the skate has a grey under surface. Further, when the under surface is upturned, as in *Remora*, it becomes dark, but no mention is made of the dorsum, which remains dark. It can hardly be supposed, however, that many species of skate have a white under surface for this purpose, though

they can dart upward very actively, nor will the explanation altogether suit the frog-fish (*Lophius*). Some of the finest silvery bluish-green or yellowish touches of the short-spined *Cottus* are under the throat. The gorgeous colours of several of the British wrasses do not appear to be either for warning or protection, nor do they appear to be connected with Sexual Selection. Moreover, it may be asked if the white under surface of many terrestrial mammals has been acquired for the same reason, viz. rendering them invisible against the sky when viewed from beneath. In connexion with this explanation it has also to be remembered that the enemies of fishes do not always look at them from these points of view. Again, freshwater and marine fishes agree in regard to this coloration, and whilst the dark dorsal surface does aid in rendering the fishes obscure, the constant movement of the tail in streams makes them obvious enough. Besides certain silvery fishes with laterally compressed bodies are very conspicuous and the ventral edge is thin. Thus in the tidal pools in May young sand-eels of 4 inches swim in parallel ranks, conspicuous by their finely iridescent green backs and silvery sides, or sport amongst the fringing seaweeds like flashes of silvery light in the sunshine. Such forms are no less conspicuous in the open sea—indeed, their only safety in this respect is immersion in sand. The dull bluish-black dorsum of the herring renders it less visible, but the approach of an enemy causes it to dart aside and expose the flashing silvery body.

Prof. Moseley gives the instance of *Antennarius*, which is coloured, like the gulf-weed (*Sargassum*), with spots of white to imitate the patches of *Membranipora*. Bright spots of white are common in young sea-scorpions, young lump-suckers, and others, but it would be difficult to draw a similar conclusion. The adult shanny and the gunnel are certainly coloured in harmony with their surroundings, just as the upper surface of many flat-fishes is. The same may be said of other blennies. Mr. Garstang cites the black dorsal fin of the weever as a warning colour, lest it should be mistaken for the gurnard. The bold touches of black and other colours on the dorsal fins of other fishes are not, however, thus to be explained.

Deep-sea fishes are black or white as if bleached (Moseley). On the other hand, the pelagic young of the conger (*Leptocephalus*) and of *Plagusia* are transparent.

The pelagic young of some fishes, *e. g.* the skulpin, have the under surface darkly pigmented, yet its habits agree with those of its fellows which have the same region translucent

or white. Some may consider, however, that such is a provision for reducing the numbers of troublesome fishes. At any rate the view that the pale under surface is protective meets with exceptions in those forms. Again, the conspicuously pigmented fins of the young mackerel midges (*Motellæ*) can scarcely be for protection, unless they mimic spines when collapsed, and the same may be said of the yellow pelvics of the young ling. Mr. Beddard thinks the bright colour and large size of the fins of certain fishes may be protective (*e. g.* flying gurnard). Another example is the sapphirine gurnard, yet in this case the protective function is doubtful.

The transparent pelagic eggs of the cod tribe, flounder tribe, and many others are supposed to escape notice by this provision, but then the young becomes conspicuously tinted before hatching, and therefore at a time when it is most important that it should be invisible. If translucency be a protection in the one case, colour under the same circumstances cannot likewise be so.

The very great variety of markings and tints in larval fishes under the same conditions shows the difficulty of drawing rigid conclusions as to protective or warning coloration in such forms, though they may be remnants of ancestral coloration. Some might be disposed to think this a crucial test of the theories propounded concerning the environment of certain forms on land. Yet the history of the changes of coloration undergone by a single species, *e. g.* the cod, shows that important purposes are subserved by these changes. Thus the minute larval cod escapes from the egg with a series of transverse bars; then the black pigment is rearranged longitudinally along the dorsum as it swims high in the water. To this is by-and-by added yellow pigment, causing (with the black) a greenish hue. When it seeks the rocky margins it becomes boldly tessellated. At a later stage it again becomes more uniformly tinted as it seeks the offshore, though some which haunt the tangle-forests are boldly blotched with reddish brown. In its adult state its sides and dorsum are mottled with yellowish green, though this does not seriously affect its uniformity. If we attempt to contrast the foregoing changes with those of the haddock, uncertainties arise. The larval haddock has no transverse bars, though bred side by side with the cod, but the dorsal band of black pigment is developed in the next stage (post-larval). Instead of seeking the shore the little haddock keeps to deep water, and it soon develops the characteristic bold touches of black on the sides above the pectoral region, the rest being uniformly

tinted with a silvery sheen and a cupreous lustre. Not till it is between 3 and 5 inches long does the haddock seek the inshore waters. To sum up: the haddock differs from the cod in its larval coloration, agrees in its post-larval, and thereafter diverges. If the tessellated condition of the cod is protective amidst the tangle-forests, what can the function of the isolated black spots on the whitish sides of the haddock be in its deep-sea retreats and as it passes when from 3 to 5 inches long to inshore waters?

Mr. Beddard and Dr. Browne Goode think the colours of certain fishes (*e. g.* rock-cod) are directly derived from red algæ through the coloured crustaceans, and Dr. Günther and Miss Newbigin have similar views in connexion with the salmon. Mr. Beddard gives as his reason that if Natural Selection had caused a change in colour, it would rather have been by an alteration of existing pigment than by the formation of fresh pigment red in colour. Other fishes, however, which feed largely on red crustaceans show no increase or alteration of their pigment, and some which do not feed on red forms of any kind may present similar pigment. Brightly coloured wrasses, such as the rainbow-wrasse, occur at considerable depths where no seaweeds are. The view of Prof. Poulton, for which he cites also the support of Prof. Herdman, that bright colours in fishes have a compensation in increased wariness, whilst protectively coloured forms are more readily caught, is interesting, but needs further corroboration.

Fishes, moreover, are a group in which it may be supposed, and Mr. Darwin has supposed, that Sexual Selection has come into play in connexion with beauty of colouring in the males. In such fishes as the salmon, lump-sucker, goby, dragonet, stickleback, and others the sexes are distinguished by marked coloration at the spawning-season, the males being then highly tinted. Moreover, the dragonet and *Arnoglossus* are examples of fishes in which the sexes are so different that they have each been described as separate species. On the other hand, fishes like the cod, haddock, herring, pilchard, and mackerel, which roam in vast shoals, are characterized by the uniformity of tints in the sexes. Recently experiments have been made with a view to test the selective powers of the female fish in certain cases, as by Saville Kent and Holt in the dragonet and by Heincke and Guitel in the gobies. On the whole these have given no certain indication of Sexual Selection on the part of the female, for she is as readily attracted by a male of sober hues as by one in all the

bravery of his conspicuous coloration. Why these bright colours are specially developed at the spawning-season is still an open question. It has been suggested they may be of use occasionally in terrifying other fishes. In the lump-sucker the bright colours do not seem to act as a warning, for the cod will in May swallow two of them, the larger about a foot long. It is interesting that the bimaculated and other suckers are often conspicuously coloured. The females do not seem to be less conspicuous in order to subserve protection for the eggs. In the case of those fishes, *e. g.* the gunnel, which attend the ova the colour is similar in both sexes.

The coloration of the large marine lizard (*Oreocephalus amblyrhynchus*) of the Galapagos Islands (500 miles west of South America) and of the oceanic turtles present few features of moment. The former is of a dirty black colour. The water-snakes, which occasionally are captured in sea-water, are often boldly banded with blackish grey and white.

Sea-birds offer few parallels to land-birds in regard to protective coloration. The great group of the gulls is more or less white and uniformly tinted in both sexes. Exceptional coloration occurs in the tern-like boatman-bird, which has two long pink feathers in the tail. The skuas, which have similar aerial habits, are often brown, and so are the petrels, whereas the gannets are yellowish white.

The swimmers, like the auks, puffins, divers, and penguins, have the dorsum dark and the under surface whitish or greyish, as in the cormorants. Many ducks and geese are similarly tinted, while others are white or black. The sexes in the ducks are boldly separated by the brighter colour of the males.

Shore-birds, again, are usually greyish and less visible in many cases, yet the oyster-catcher is prominently speckled.

With the exception of the shore-birds, it cannot be said that the coloration of sea-birds is protective.

In connexion with the highest group, that of the marine mammals, it has been stated by Mr. Wallace and others that the black and white colours of the dorsum and under surface of porpoises have been acquired for protection (on the same principle as already mentioned in the fishes); but this distribution of colour would not avail them against their greatest destroyers, the killers, which swim on a level with them. The dark brownish-grey hue of the seals in the water avails them no better, for they are likewise captured by the killers. The colour of the larger whales, again, is similar to that of

the porpoises, and some, like the killer, are boldly blotched with white, as also is the arctic seal. Moreover, the hump-backed whale (*Megaptera longimana*) has pure white flippers 12 feet long, whilst the smaller rorqual has a bold white band across the flipper. The well-known *Beluga* is dull whitish all over. As all cetaceans come to the surface to breathe, they must frequently expose a black or brownish-black surface. Now black is a tint which is conspicuous in the sea, and accordingly the fishermen use black flags in preference to white on their dandys, since they are so easily recognized in the darkness or dull light of the early morning. That black should be a protection to these animals, and that species are whitish all over or have pure white flippers or bands, is a condition of things creative of uncertainty in regard to the theories alluded to. The bold white touches, for example, of the killer can scarcely be held to be recognition-markings, like the white tail of the rabbit. The variegated hues of the arctic seal may subserve protection. If they do, those of other colours are at a disadvantage. Considerable variety, indeed, occurs in the group; thus the elephant-seal is dull greyish above, light beneath, and the sea-leopard is spotted yellowish white and dark grey on the back, with a yellowish under surface. The sirenians are dull brownish dorsally and ventrally, so that the lighter hue seen against the sky is absent in their case; but, on the other hand, they are not oceanic.

A general survey of the coloration of marine animals raises doubts as to the interpretations which have been brought forward to explain it. Some of these explanations, it is true, are more or less in agreement with facts; but, so far as can be seen, other facts are adverse, and demonstrate the extreme caution necessary in dealing with such interpretations. Before anything definite can be produced a much more extensive, more exact, and long-continued series of observations on the subject is imperative. That the coloration, often so varied and so beautiful, is of importance to marine animals can scarcely be doubted, for Nature is ever prescient; but it is not always easy to adapt the theories of the day to her workings.